Füchse registriert werden. In 20 dieser Städte sind Fuchsbaue mit Jungenaufzucht im Siedlungsraum bekannt. Dabei werden Stadtfüchse überproportional häufger in größeren Städten als in kleineren Ortschaften beobachtet. In Zürich, der größten Schweizer Stadt, waren gemäß der Jagdstatistik bis zu Beginn der 1980er Jahre Stadtfüchse sehr selten. Erst ab 1985 begann die städtische Fuchspopulation markant anzusteigen. Auch die umliegenden ländlichen Gebiete verzeichnen ab 1984 eine deutliche, allerdings weniger starke Zunahme der Fuchsbestände, die u.a. mit der erfolgreichen Tollwutbekämpfung zusammenhängt. Als Erklärung der Präsenz von Füchsen im Siedlungsraum, einem bisher vor allem aus Großbritannien bekannten Phänomen, schlagen wir zwei alternative Hypothesen vor, welche einerseits den Populationsdruck in ländlichen Gebieten, andererseits stadtspezifsche Verhaltensanpassungen der Füchse ins Zentrum stellen. Fuchspopulationen im Siedlungsraum beeinflussen das Verhalten und die Einstellung der Bevölkerung gegenüber Wildtieren und haben Konsequenzen für das Fuchsmanagement und den Umgang mit Zoonosen, wie Tollwut und alveoläre Echinokokkose.

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Original investigation

Feeding selectivity and food preference of *Ctenomys talarum* (tuco-tuco)

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Abstract

We tested feeding selectivity and food preference of *Ctenomys talarum* (tuco-tuco). To test feeding selectivity, above ground and below ground plant biomass from the field was determined and botanical composition of the diet was estimated in stomach contents using microhistological techniques. Feeding preferences were studied carrying out laboratory cafeteria experiments. *Ctenomys talarum* behave as generalist and opportunistic herbivores consuming the greater part of species present in the grassland. The above ground portion was preferred over the subterranean one. Grasses constituted 94% of the above ground vegetative fraction consumed and were generally selected. Preference trials also showed that *C. talarum* prefer above ground parts of grasses to other choices.

Key words: *Ctenomys talarum* diet, feeding selectivity, food preference

Introduction

Rodents of the genus *Ctenomys* (tuco-tucos) are subterranean herbivores whose populations are distributed in a discontinuous pattern throughout Argentina, Paraguay, Bolivia, Uruguay, Perú, Chile, and southern Brazil (WOODS 1984). Most herbivores inhabit a biotope in which the food plants are more or less continuously distributed in space and time, and whose accessibility is restricted by the structural and chemical properties of the vegetation (ILLIUS and GORDON 1993). They select food items according to their preference, and availability in the field. Preference is the predilection of a consumer for a particular class of food, and it is the result of how well the consumer "likes" this food relative to other ones, when all are equally available (NORBURY 1992). Diet selection in herbivores may be explained by models where the rate of intake is maximized with nutrient constraints, toxins are avoided or their intake is minimized (STEPHENS and KREBS 1986). A foraging herbivore maximizes its nutrient intake when greater nutrient intake converts directly into greater survival and reproduction (nutrient maximization; BELOVSKY and SCHMITZ 1994).

Food resources have been implicated as important to both burrow location and burrow

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system size, suggesting that foraging is a critical component of ecology of subterranean rodents (BUSCH et al. 2000). In terms of nutritional value, below ground plant tissues may represent a more variable resource than above ground tissue (ANDERSEN 1987). This fact and the high energetic costs of digging may influence food selectivity. HETH et al. (1989) proposed that subterranean herbivores cannot afford to be selective feeders since search costs would exceed the benefits of being selective, therefore they should utilize all food that they encounter. Furthermore, subterranean rodents are expected to consume a great proportion of below ground vegetation (VLECK 1979).
Diet selection by herbivores is important in determining their effects on plant communities. Empirical evidence and theoretical models suggest that generalist herbivores may have more widespread effects on plant communities than specialist herbivores, since they can greatly reduce, or even eliminate, some plant species while persisting on the remaining species. Much remains to be learned regarding the foraging ecology of subterranean rodents. Cafeteria-style test of food preference would help to determine the nature and extent of dietary specialization. In addition, field studies of foraging behavior would allow to test optimal foraging models (STEPHENS and KREBS, 1986) under the condition faced by free-living animals.
This study assesses different aspects of the feeding behavior of individuals of a *Ctenomys talarum* population inhabiting a coastal dune grassland in the southeastern Buenos Aires province, Argentina. Specifically assessed are: 1) *C. talarum* feeding selectivity in the field, and 2) food preferences of *C. talarum* in cafeteria test.

Material and methods

Two studies were conducted. One was carried out in the field to evaluate *C. talarum* feeding selectivity. The other was a cafeteria test developed to determine if food quality (fiber/protein) determines their feeding preference.

Feeding selectivity (field data)

The study was conducted on coastal dunes at Mar de Cobo (Buenos Aires Province, Argentina), in a natural grassland with the predominance of perennial grasses (COMPARATORE et al. 1991).
Vegetation and animals were sampled in autumn, winter, spring, and summer. Fifty seven animals were kill-trapped and their stomachs removed. Because above ground foraging occurred near the burrow opening, for each animal captured, four vegetation samples were collected from around the opening (30 cm diameter and 30 cm depth). Above ground and below ground samples were separated and dry plant biomass was estimated and expressed as percentage of total biomass. In addition, the percentage of the above ground fraction of each species was computed.
The botanical composition of *Ctenomys talarum* diet was estimated using microhistological techniques. Stomach contents were processed individually according to WILLIAMS (1969), and the botanical composition of the diet was quantified according to SPARKS and MALECHEK (1968). The subterranean, above ground and reproductive fractions were quantified. In addition, the species percentages in the vegetative fraction were determined, since it is the only one in which fragments could be differentiated to species level.
The seasonal percentages of the components of *Ctenomys* diets were compared using a Kruskal-Wallis test ($P = 0.05$). Diet and grassland botanical composition were contrasted, establishing animal selectivity for total above ground and subterranean fractions. Reproductive fraction selectivity could not be established because its percentage was not determined in the grassland. In addition, selectivity for the above ground vegetative fraction of the species in the diet was computed.
The following index (KRUEGER 1972) was used to determine relative species selectivity:

$$SI = \%\ Di \times fdi / \%\ Pi \times fpi,$$

where % Di and fdi are the seasonal mean percentage and the frequency of component i in the diets, and % Pi and fpi are the seasonal mean percentage and the frequency of the component i in the grassland. Chi square with 95% confidence was used to determine if the seasonal SI for each component was significantly different from 1. Kulcyznski's similarity index (HOLECHEK et al. 1984) was used to evaluate the similarity of diets and pasture. The species considered in the analysis were those whose seasonal mean percentage by the frequency, in the diets and/or in the grassland, were over 2%. Results are shown as mean ± SD (standard deviation).

Feeding preference (cafeteria test)

Animals for the experiments were live-trapped in the coastal dunes of Necochea (Buenos Aires province). Food preference was investigated in the laboratory by the amount of plant matter consumed during feeding trials (PHILLIPSON et al. 1983). To conduct the trials, animals were set in a feeding apparatus (42×42×6 cm) which consisted of a central nest box with an opening in each of four feeding arenas. The gridded floors of the feeding arenas allowed food remains and faeces to drop into a collecting tray without being moistened with urine.

Leaves and stems of plant species for the experiment were collected at the same site where the animals were trapped. Potatoes and carrots, which have low fiber percentages, were also used as choices. Standard cafeteria trials were conducted performing three different tests. In each one the same wet weight of four different kinds of food was offered simultaneously. Each test lasted for four days with 10 repetitions using different individual tuco-tucos (5 adult females and 5 adult males). Every day equal wet weight of each plant choice was offered. Intake was calculated on both a fresh-mass and a dry-mass basis. The residual plant material was sorted and weighed on succeeding days and the difference recorded. Then, it was dried at 70–80 °C to invariable weight. Conversions of fresh mass to dry mass were calculated from samples of plant material that was maintained in empty cages during the trials.

Each choice of food was weighed to the nearest 0.01 g and offered in different compartments of the feeding apparatus. The position of the foods varied at random. Species chosen for the cafeteria test are present in the natural diet of *Ctenomys talarum* in Necochea, except for *Ipomea batatae* and *Daucus carota*.

To test if dietary preference correlates with some particular portion of the plant we offered different parts of two species of grasses that appeared in the field diet: *Cynodon dactylon* stem, *C. dactylon* leaf, *Bromus unioloides* stem, *B. unioloides* leaf. To test if the preference has a relation with the fiber content of the choice *C. dactylon* stem, *B. unioloides* stem and *Ipomea batatae* tuber and *Dacus carota* root (fiber content: 17% and 13%, respectively) were offered. We also tested the preference for forbs or grasses and different parts of them, offering two species from the field diet: *Hydrocotile bonariensis* (forb) above ground portion *H. bonariensis* below ground portion, *Panicum racemosum* (grass) above ground portion, *P. racemosum* below ground portion.

Protein content was determined by the microbiuret method (GORNALL et al. 1949) and fiber content was determined by the GOERING and VAN SOEST (1970) technique. Results are shown as mean ± S. D. A non-parametric multiple comparison test (ZAR 1984) was used to ascertain the significance of the preferences observed. Chi square with 95% confidence was used to test whether the proportions of food consumed were equal to expected frequencies, based on the relative dry weight of food offered.

Results

Feeding selectivity

Comparison of botanical composition of grassland and diet

Proportion of subterranean biomass was not significantly different from the above ground ($P > 0.05$; Fig. 1 a). Perennial grasses dominate the grassland biomass (79% of total above ground available biomass). The proportion of perennial monocotyledoneans decreased in spring, while annual monocotyledoneans increased; annual forbs decreased in autumn and perennials in winter (Fig. 2 a). Monocotyledonean composition was dominated by *Panicum racemosum*, which constituted 25% of the annual biomass.

Analysis of the contents of 57 stomachs revealed that tuco-tucos exploited at least 16 species of plants annually. The above ground vegetative portion of plants predominated (84.5%) in the annual diet, whereas subterranean and reproductive portions constituted only 11% and 4.5%, respectively (Fig. 1 b). Grasses comprised the highest proportion of the annual diet. Its average annual occurrence was 94% of the annual above ground vegetative fraction (Fig. 2 b). *Bromus unioloides* (46%), *Panicum racemosum* (16%), and *Poa bonariensis* (10%) were consumed more intensively, as they constituted 72% of the dry weight of the annual diet.

Seasonal changes in diet

Although perennial grasses comprised the highest proportion of the diet year round (Fig. 2 b), consumption preference of differ-

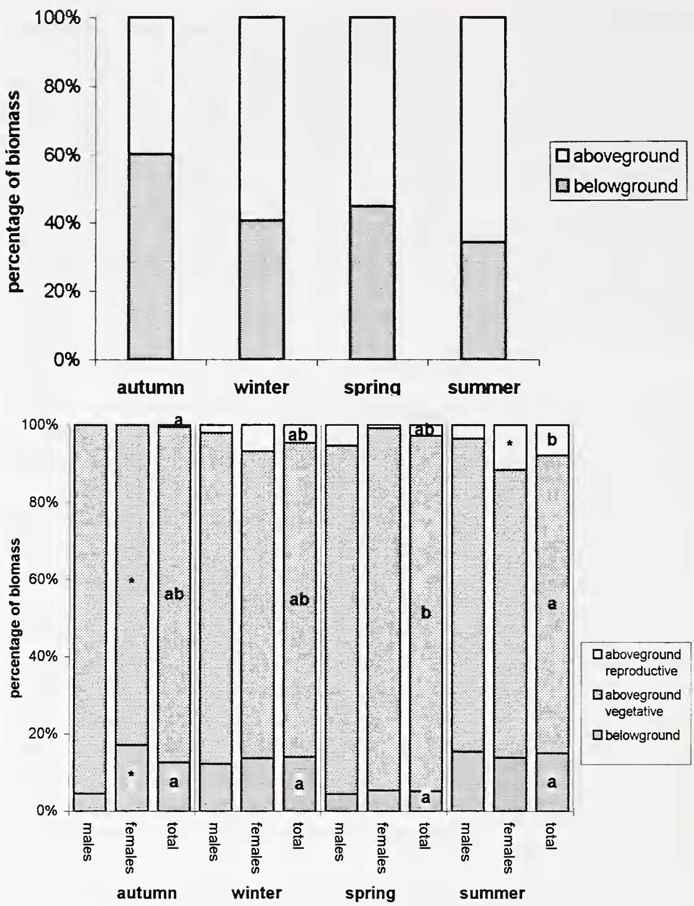

Fig. 1. Percentages of biomass in the grassland and in the diet of tuco-tuco: a) Above ground and subterranean percentage of plant biomass in the natural grassland at Mar de Cobo where *Ctenomys talarum* was trapped; b) Above ground, reproductive and below ground percentage of plant biomass in the stomach of *Ctenomys talarum* trapped in a natural grassland at Mar de Cobo.
Different letters indicate significant differences between seasons; * indicates significant differences between sexes in each season.

ent species varied. Thus, the analysis of the seasonal diet of the tuco-tucos revealed that *Bromus unioloides* was an important source of nutriment almost year round, but it was consumed less during the autumn season. On the other hand, only during spring *Panicum racemosum* ceased to be an important component of the tuco-tuco's diet. *Poa bonariensis* was consumed more in autumn, spring, and summer and less in winter. The perennial forb *Adesmia incana* became an important component in the spring diet (10%). Although there were no significant differences between the average of the below ground fraction consumed in each season ($P > 0.05$); the mean consumption (5.3 ± 4) in spring was lower than in the other seasons (Fig. 1 b).

Effect of sex on diet

Males seem to be more selective than females (male and female diets show a 58% and 66% similarity with the grassland, respectively; Kulcyznski's index). Differences were noticed in winter and in summer when male and female diets exhibited statistical differences in the proportion of *Bromus unioloides* ($P < 0.02$). Moreover, plant fractions were consumed differentially (Fig. 1 b). Whereas males consumed the subterranean and vegetative fractions of plants in the same proportions year round, females did not ($P < 0.02$). Furthermore, in autumn females consumed a higher proportion of the subterranean fraction ($P = 0.006$) and smaller proportion of the above ground vegetative ($P = 0.004$) than males, and during sum-

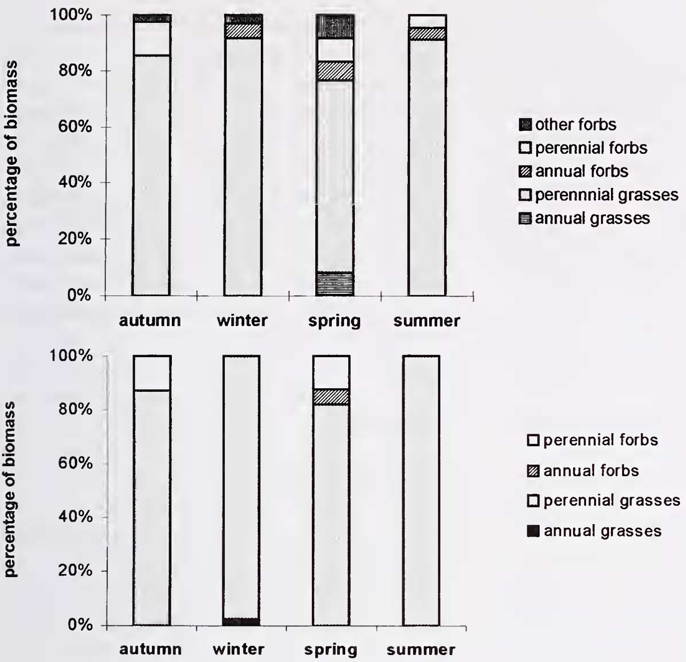

Fig. 2. Botanical composition of the grassland and of the diet of tuco-tuco: a) Percentage of biomass of above ground available vegetation on a natural grassland at Mar de Cobo; b) Percentage of biomass of different types of above ground vegetation in stomachs of *Ctenomys talarum*.

Table 1. Seasonal values of selectivity index (SI) for each above ground vegetative food item and for the subterranean fraction. (*) denotes statistically significant difference from 1 (SI ≠ 1) Chi-square test (P = 0.05)

	AUTUMN N = 15	WINTER N = 15	SPRING N = 12	SUMMER N = 15
Above ground fraction				
Annual grasses	–	–	0	–
Perennial grasses	1.01	1.06	1.19	1.09
Annual forbs	–	0	0.84	0
Perennial forbs	1.07	–	1.46	0
Subterranean fraction	0.32*	0.35*	0.12*	0.44*

mer they consumed a significantly higher proportion of reproductive structures than males (P = 0.028; Fig. 1 b).

Relative plant selectivity

Tuco-tuco ingested perennial monocots and dicots in proportion to their mass (Tab. 1), and thus according to the probability of encountering them. Nevertheless, tuco-tucos are capable of selective foraging, since the above ground fraction of the plant was not selected by individuals of both sexes in all seasons (P < 0.05). In addition, the analysis of the stomachs showed that tuco-tucos select some monocots species with preference changing seasonally; the grass *Bromus* was selected in winter, spring, and summer but was indifferent in autumn, whereas *Poa* was selected in autumn, spring, and summer but not in winter. *Panicum* was preferred in autumn and avoided in other seasons (P = 0.05). Furthermore, males and females showed different feeding selectivity for *Bromus unioloides*, thus, it was selected in winter and summer by males, but not by females (P = 0.05).

Feeding preference

Tuco-tucos consumed 200 ± 57 g ind^{-1} d^{-1} of food, and 8 ± 3 g protein and 26 ± 53 kcal per day. The experiments demostrate that *C. talarum* is able to discriminate among the plant species tested, and harvested grasses selectively. Although some species and/or part of the plant were consumed more than others (Tab. 2), tuco-tucos consumed all plants offered in the test and consumption of choices other than the preferred ones make an important contribution to total ingested nutrient (7–44% protein). Results indicate preference for above ground portions of grasses over other choices tested. Furthermore, plant portions with a low fiber/protein ratio were less preferred than those with a high fiber/protein ratio. When offered as above ground samples, significant quantities of all grasses were consumed by the tuco-tucos and no preference for stems or leaves was detected, but as noted above a preference for low quality food was noticed, thus the *B. unioloides* leaf, which has the lowest fiber/protein ratio, was eaten to a lesser proportion than the other choices (Tab. 2 a). When offered monocots (*B. unioloides*, *C. dactylon* or *P. racemosum*) and other choices, grasses represented 70–90% of the total consumption and grass stems were preferred to other choices tested (Tab. 2 b, c). This preference was independent of the nutritional quality of the other choice, thus the stems of grasses with a higher fiber/protein ratio were preferred to *I. batatae*, *D. carota* or to *Hydrocotyle bonaroensis* above ground proportion (Tab. 2 b, c).

Discussion

Feeding selectivity

Ctenomys talarum behave as a generalist and opportunistic herbivore since it consumes the greatest part of the species present in the grassland, and changes its diet in relation to food availability. Similar food habits were reported for other *Ctenomys* species (*C. australis*, COMPARATORE et al. 1995 and *C. mendocinus*, MADOERY 1993) and other subterranean rodents such as

Table 2. Dry weight consumption and fiber/protein ratio of food items for three different cafeteria tests. (a) First cafeteria test compared the consumption between different portions of two species of grasses; (b) second cafeteria test compared the consumption between items with high and low fiber/protein ratio; (c) third cafeteria test compared between subterranean and above ground fraction of forbs and grasses. Non parametric multiple comparisons test to differentiate among preference fractions (small letters) (P = 0.05).

SPECIES	QUANTITY EATEN g/day ± SD	FIBER/PROTEIN RATIO
(a)		
B. unioloides leaf	11.29 ± 4.79 a	2.42
B. unioloides stem	24.93 ± 11.61 b	7.41
C. dactylon leaf	23.63 ± 12.26 ab	2.44
C. dactylon stem	28.87 ± 12.69 b	5.56
(b)		
B. unioloides stem	32.35 ± 16.3 a	7.41
C. dactylon stem	31.55 ± 14.21 a	5.56
I. batatae	4.65 ± 2.18 b	3.50
D. carota	2.87 ± 1.72 b	1.57
(c)		
H. bonariensis above ground	8.6 ± 2.26 a	2.27
H. bonariensis subterranean	15.42 ± 12.21 ab	11.06
P. racemosum subterranean	17.23 ± 4.07 bc	14.89
P. racemosum above ground	39.33 ± 25.57 c	8.11

Thomomys talpoides (STUEBE and ANDERSEN 1985), *Geomys attwateri* (WILLIAMS and CAMERON 1986), *Heterocephalus glaber* (BRETT 1991) and *Spalax ehrenbergi* (NEVO 1979). This behavior would be adaptive for a mammal that supports a high cost of burrowing and poor available energy (HETH et al. 1989). In general, the food habits of *C. talarum* at Mar de Cobo appear to be similar to those reported for *C. talarum* at Necochea (COMPARATORE et al. 1995). Individuals of both populations preferred monocotyledoneans, but tuco-tucos consumed large amounts of *Bromus* at Mar de Cobo and of Poa at Necochea (COMPARATORE et al. 1995), suggesting that modifications in the diet may be influenced by changes in food offered. Given the high cost of burrowing (VLECK 1979) it is not surprising that tuco-tucos shift their diet in accordance with habitat availability.

C. talarum selected the above ground fraction of plants. This may be due to the fact that tuco-tucos live in areas where plant species have different life cycles, therefore the above ground fraction would be available all year round. On the other hand, the lowest consumption of the subterranean fraction during spring is in relation with the active growth of the above ground fraction in this season. WILLIAMS and CAMERON (1986) indicated that the difference in the subterranean and above ground proportion of plants in the diets of pocket gophers is related to the different behavior of the animal species. The above ground proportion would be higher in those groups that spend more time out of their burrows. In this sense although tuco-tucos forage within their tunnels, they feed mostly above ground by venturing away for their tunnels for brief periods to gather plant parts from the surface. The vegetation in the vicinity of their holes commonly shows evidence of their feeding activities (REIG 1970).

At Mar de Cobo where densities were high (65 ind./ha), reproductive structure consumption was minimal (4%), whereas at Necochea (13 ind./ha) it played an important role in *Ctenomys* diet (38% of total; COMPARATORE et al. 1995). This suggests that the proportion of high caloric food is higher in animals living in populations of low density. BUJALSKA (1983) reported a similar relationship between density and diet quality for *Clethrionomys*, a forest dwelling microtine.

The diet of tuco-tucos depends on sex, as females appeared to be less selective than males. The larger consumption of reproductive plant structures by females could respond to higher protein requirements for lactation. Differences in preference by reproductive females have been reported for other subterranean mammals like *Geomys attwateri* (WILLIAMS and CAMERON 1986) and *Spalax erhenbergi* (NEVO 1991).

Feeding preference

Choice tests support the fact that *Ctenomys talarum* is a herbivorous generalist with a preference for the above ground fraction of grasses. Thus, although some items were preferred, the diet was supplemented with other choices. In this manner, a varied diet was maintained, even with the abundance of the preferred food resource and without differential foraging costs. Herbivores may select a diet that mixes different types of dietary items to balance the intake of nutrients required for proper growth or successful reproduction (REZSUTEK and CAMERON 1998).

If we accept 200 g fresh weight as an average daily consumption, tuco-tucos intake would amount to 2600 g and 13000 g fresh vegetation per ha consumed each day at Necochea and Mar de Cobo, respectively. This amounts to 996–4680 kg per ha per year, not including vegetation stored uneaten or used to build nests. Tuco-tuco total energy intake per day was comparable to data reported for the subterranean rodent *Thomomys talpoides* by STUEBE and ANDERSEN (1985).

In our experiments, grasses provided not only most of the daily energy and protein requirements, but also with more than 80% of the daily dietary fiber. As tuco tucos are coprophagous rodents with a large caecum (11% of the gut), they are able to optimize